

Structure of female genitalia of glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae)

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Abstract

The functional reproductive morphology of the female glassy-winged sharpshooter, *Homalodisca coagulata* (Say), is described at both light microscopy and scanning electron microscopy levels. The female has nine abdominal segments; the seventh to the ninth abdominal segments are modified for reproduction; the eighth tergite is reduced to two segments, with the ovipositor partially exposed from the modified ninth segment—the pygofer. The pygofer, covered with trichoid and coeloconic sensilla, almost completely encloses the ovipositor, which consists of three pairs of valvulae and two pairs of valvifers. The first and second valvulae function together for oviposition. The first valvulae are located exterior to the second valvulae, both of which bear many trichoid, campaniform, and coeloconic sensilla. The third valvulae, possessing many coeloconic sensilla, envelope the first and second valvulae. Seven major muscles are found to be associated with the ovipositor and the pygofer. The oviposition process is described with respect to the activity of the valvulae and their associated musculature. The female morphology follows the general pattern of cicadellids as a group.

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The glassy-winged sharpshooter (GWSS), *Homalodisca coagulata* (Say), is a serious pest of many tree and vine crops and is known to vector the bacterium *Xylella fastidiosa* (Turner, 1949), which cause Pierce's disease of grapes (Alderz and Hopkins, 1979; Hewitt et al., 1946), almond leaf scorch, and oleander leaf scorch (Costa et al., 2000; Davis et al., 1980). *H. coagulata* currently is considered to be the most significant insect pest threatening the California grape industry (Purcell, 1999; Purcell and Saunders, 1999). *H. coagulata* belongs to the tribe Proconiini of the subfamily Cicadellinae, family Cicadellidae. All members of the Proconiini tribe are xylem feeders (Nielson, 1979).

The biology, particularly the reproductive morphology and physiology, of *H. coagulata* remains largely unknown. Sanderson (1905) observed that the insect has two to three generations per year in Texas, and the adults hibernated in 'rubbish' on the ground near food plants. Eggs were deposited side-by-side in batches of 10–15 eggs forming a 'blister' under the leaf surface (Sanderson, 1905). Turner and

Pollard (1959), using yellow sticky board traps to study field populations of *H. coagulata* in Georgia, found that the insect had two full generations per year, followed by a partial third generation. They also indicated that the egg masses were deposited under the epidermis of the leaf in groups of eggs ranging from 11 to 20 (Turner and Pollard, 1959). Bivoltine patterns of *H. coagulata* occur in Florida (Alderz, 1980) and southern California (Blua et al., 1999) with an occasional third generation in Georgia (Turner and Pollard, 1959).

This study was conducted to document the morphological and anatomical structures associated with the reproduction of female *H. coagulata* at both the light microscopy and scanning electron microscopy levels. A description of the morphology and function of the musculature associated with the ovipositor is also presented. Scanning electron microscopic examination of the ovipositor revealed sensilla that may play a role in *H. coagulata* host selection, particularly in regulating the patterns of movement between hosts, hence serving as a mechanism in the selection of appropriate hosts for oviposition. Knowledge of host selection criteria and associated mechanisms is critical in controlling vector insect populations. This research may contribute to a better understanding of possible host selection mechanisms of *H. coagulata* and ultimately the development of methods to suppress California *H. coagulata* populations.

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1. Materials and methods

1.1. Light microscopy

Specimens were collected primarily in the summer of 2001 from citrus at the University of California, Riverside Agricultural Operations (UCR Ag Ops). For light microscopic study, the specimens were immediately injected with 70% ethanol into the abdomen using a micro-syringe, and then stored in 70% ethanol until dissected. Dissections were conducted under a stereoscope (Model MZ12.5, Leica Microsystems Inc., Bannockburn, IL) fitted with a light source (Model L2, Leica Microsystems Inc., Bannockburn, IL) and a camera lucida attachment (Model 10446193, Leica Microsystems Inc., Bannockburn, IL). A second light source (Model, 3600, DiAx, Tensor Corp., Brooklyn, NY) was used to illuminate the drawing surface. Drawings were labeled using Adobe Illustrator software (Adobe Systems Incorporated, San Jose, CA). Approximately, eighty specimens were dissected for observation. Additional mounted slides of the segments of the ovipositor and abdominal segments were prepared and then used to examine the morphology and to generate drawings. Four specimens were measured using an ocular micrometer fitted to the stereoscope to determine the dimensions of abdominal segments.

The system developed by Snodgrass (1933) was followed to name the structures, excluding muscles. The musculature was studied and muscles were named according to their function. Clay models were prepared during the study to clarify the relationship of segments with each other and the consequences of muscular action during oviposition. Video footage of two rounds of *H. coagulata* oviposition was kindly provided by Dr Raymond Hix (Pers. Comm.), and was used to help determine the possible sequence of primary muscular action during oviposition.

1.2. Scanning electron microscopy

H. coagulata specimens collected from UCR Ag Ops from 2001 to 2004, were stored and dissected in 70% ethanol. Specimens were then ultrasonically cleaned in 95% ethanol, soaked overnight in hexane, and dried on Whatman No. 1 filter paper (Whatman, Inc., Florham Park, NJ) in a covered petri dish for at least 2 days. Specimens were mounted on aluminum stubs (Ted Pella, Inc., Redding, CA) using adhesive tabs (Ted Pella, Inc.); and finally coated with palladium gold for 90 s using a sputter coater (Denton Vacuum Desk II Cold Sputter-Etch Unit, Denton Vacuum, Moorestown, NJ). The prepared specimens were then viewed with a scanning electron microscope (S3500N SEM, Hitachi, Schaumburg, IL). Some specimens were dehydrated through a graded series of ethanol and then critical point dried (Samdri 780A, Tousimis, Rockville, MD) for examination of sensilla.

2. Results

2.1. Abdominal segments and pygofer

The female abdomen (mean \pm SD length = 5.749 ± 0.402 mm) consists of nine segments including the pygofer (Fig. 1). In the dorsal view, tergite-I is folded and hidden beneath tergite-II. Tergite-II is narrow in length (mean \pm SD length = 0.270 ± 0.017 mm) and width (mean \pm SD width = 1.035 ± 0.078 mm) (Fig. 2). Tergite-III through tergite-VII, following in sequence, from anterior to posterior, are approximately equal in length (mean \pm SD length = 0.774 ± 0.057 mm) (Fig. 1). The width of the tergites increases from tergite-II, reaching a maximum width at tergite-V (mean \pm SD width = 2.993 ± 0.121 mm), and decreasing thereafter posteriorly to the pygofer (mean \pm SD width = 1.213 ± 0.084 mm) (Fig. 1).

The ventral view shows that paratergite-III through paratergite-VIII are similar in shape, all being longer (mean \pm SD length = 0.883 ± 0.039 mm) than wide (mean \pm SD width = 0.539 ± 0.037 mm) (Fig. 3) (ratio = 1.63:1). Sternite-I is partially hidden by sternite-II, and both sternites are narrower in length (mean \pm SD length S-II = 0.163 ± 0.026 mm) than the posterior sternites (Fig. 3). Sternite-III through sternite-VI are approximately equal in length (mean \pm SD length = 0.867 ± 0.061 mm) and width (mean \pm SD width = 1.519 ± 0.043 mm) (Fig. 3). Sternite-VII is elongated, with a v-shaped serration on the posterior edge (mean \pm SD length = 1.364 ± 0.033 mm), and conceals the base of the pygofer (Figs. 3 and 4), the genital chamber, and the base of the ovipositor (Fig. 6). Sternite-VIII is reduced to lip-like folds that are visible in ventral view after sternite-VII is removed (Fig. 7). The ventral view of the distal end of the abdomen also shows that the third valvulae are enveloped by the pygofer (Fig. 4) and are located ventrally with respect to the anal stylus (Fig. 5).

2.2. Pygofer

The pygofer is the modified ninth abdominal segment (Figs. 11 and 34). It is narrower posteriorly than anteriorly and is one continuous segment dorsally (Fig. 1), but is split down the body mid-line ventrally (Figs. 3 and 4). The anterior region of the pygofer articulates ventrally with the second valvifer at one ramus (Fig. 34), which is located interiorly with respect to the ramus of the second valvula (Fig. 9). The outer surface of the pygofer has many spines posterior to ramus 5 (Fig. 37). The epiproct, paraproct and anal stylus are located above the pygofer (Fig. 5).

2.3. Genital chamber

The genital chamber is located ventrally between sternite-VII and sternite-VIII (Figs. 6 and 7). It is mostly membranous and is folded into the body cavity (Fig. 7).

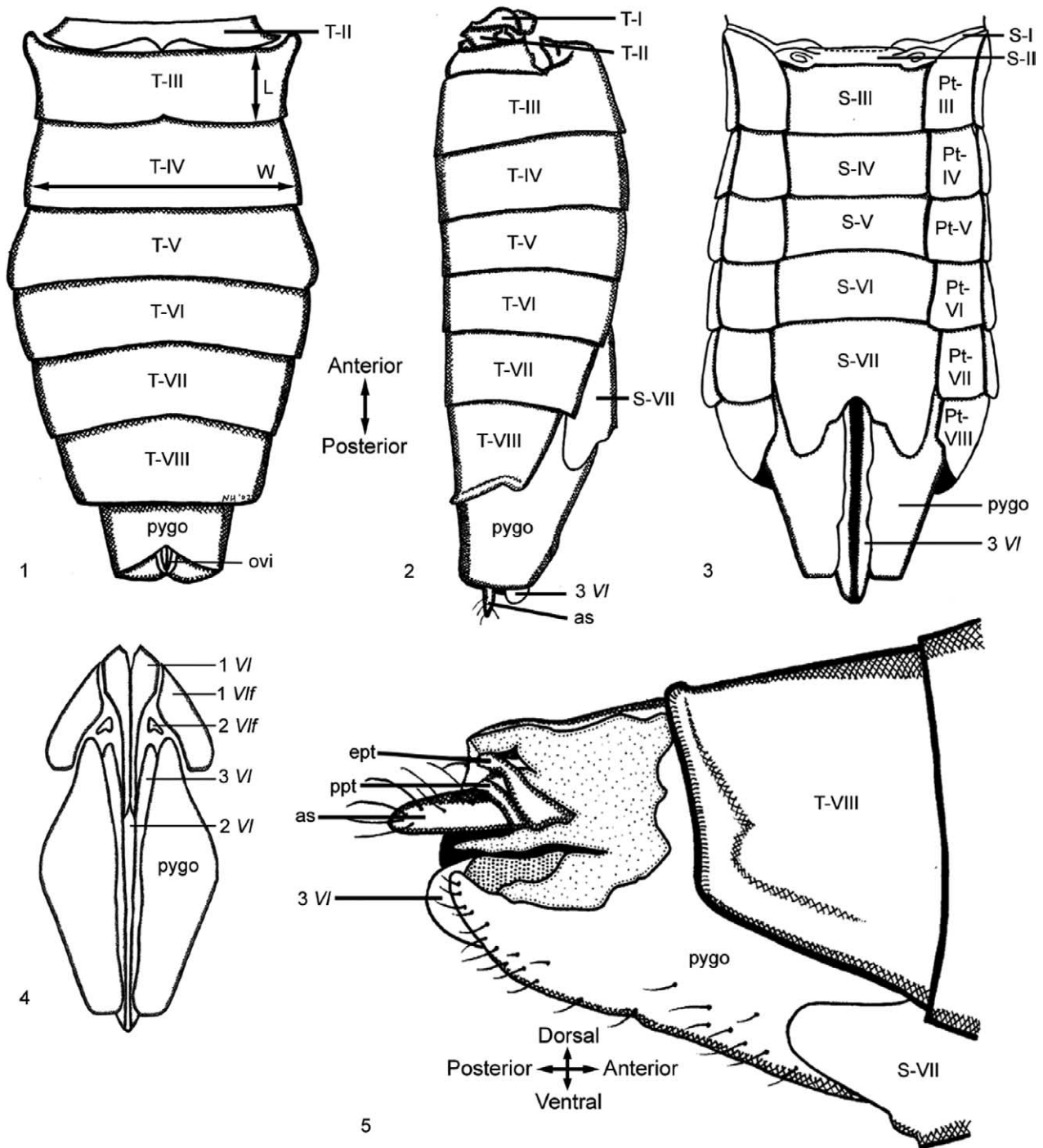


Plate 1. Abdominal segmentation of a female *H. coagulata*. (1) Tergites (T) in dorsal view; note that tergite-II (T-II) completely covers tergite-I; L: length, ovi: ovipositor, pygo: pygofer, and W: width. (2) Tergites (T) in lateral view, along with pygofer (pygo), sternite-VII (S-VII), third valvula (3 VI), and anal stylus (as). (3) Sternites (S) and paratergites (Pt) in ventral view along with pygofer (pygo) and third valvulae (3 VI). (4) Ventral view of the distal portion of the abdomen, with sternite-VII removed, illustrating the base of the first valvulae (1 VI), first valvifer (1 Vlf), second valvulae (2 VI), second valvifer (2 Vlf), third valvulae (3 VI), and pygofer (pygo). (5) Lateral view of the distal portion of tergites (T) with pygofer (pygo) partially removed to reveal epiproct (ept), paraproct (ppt), anal stylus (as), and third valvula (3 VI); S-VII: sternite-VII.

2.4. Ovipositor

The female ovipositor consists of two pairs of valvulae and their corresponding two pairs of valvifers, which are enclosed by a third set of paired valvulae (Fig. 4). Each

valvula has a ramus articulation point with a valvifer. The movement of each individual valvula is facilitated by contraction of muscles that insert on the first and/or second valvifer. All three pairs of valvulae are further externally enclosed by the pygofer (Fig. 4). The base of the ovipositor

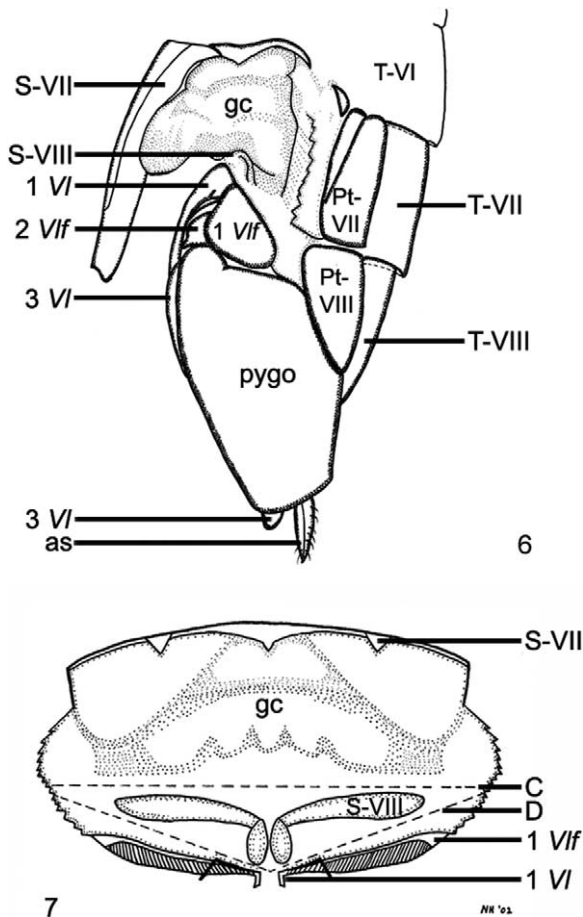


Plate 2. The genital chamber (gc) of a female *H. coagulata*. (6) A lateral view of the genital chamber (gc) of a female *H. coagulata*, with sternite-VII (S-VII) partially removed to show the reduced sternite-VIII (S-VIII), the genital chamber (gc), the base of the first valvulae (1 VI); 3 VI: third valvula, 1 Vlf: first valvifer, 2 Vlf: second valvifer, as: anal stylus, Pt: paratergite, pygo: pygofer, and T: tergite. (7) A ventral view of the genital chamber (gc), with sternite-VII (S-VII) lifted to reveal sternite-VIII (S-VIII); line C indicates a 90° bend from the internal fold, and line D indicates a 45° bend from the internal fold; 1 Vlf: first valvifer, and 1 VI: first valvula.

becomes visible when sternite-VII is removed (Fig. 4). The first and second valvulae are connected laterally by a tongue and groove mechanism (Figs. 8 and 15 black arrow), which enhances the support of muscular movement of the valvulae during oviposition. The arrangement of the valvulae with respect to each other beginning from outside to inside is described as follows: the third valvulae enclose the first valvulae which enclose the second valvulae. The ovipositor serves to cut the leaf epidermis and create a pouch into which the egg is deposited. It also serves as the tube through which the egg travels during oviposition.

2.5. First valvulae

The paired first valvulae are connected basally by a membrane. Distally they split and lie outside the paired second valvulae (Figs. 4 and 15). The first valvulae articulate with the first valvifers at two rami, one interior (r1) and one

exterior (r2) (Fig. 8). The blade-shaped first valvulae (Figs. 8 and 15) are pointed at the apex (Fig. 19), with the distal margins possessing many small denticles with smooth margins (Figs. 15 and 19 arrow). The distal tip of the first valvulae is coated with scales (Fig. 19). Numerous square-shaped plates (5 μ m in length and 5 μ m in width) (Fig. 18) form a comb on the outer margin of the first valvulae. However, the first valvulae appear to be largely smooth and free of surface sculpturing basally (Fig. 15). The morphology of the first valvulae suggests that they are exerted making the initial contact with the leaf surface and anchoring the ovipositor in the leaf surface during oviposition.

2.6. Second valvulae

The paired second valvulae lie laterally in a groove (Fig. 15 black arrow) of the first valvulae. The second valvulae dorsally articulate with the second valvifers at one ramus (r3) (Fig. 9). They are long and narrow, with the appearance of a curved saw blade (Fig. 9). About one-fourth of the length distally, the second valvulae broaden and have 38 serrated denticles on the dorsal margin (Figs. 12, 13, 15, 21 and 26). There is a distinct notch at the base where the serrated denticles begin (Fig. 9). A number of different types of spine-bearing scales are observed on the inner surface of the second valvulae (Figs. 21–24). The shape and orientation of these spine-bearing scales changes longitudinally and laterally across the inner surface of the second valvulae (Figs. 22–24). The distal tips of the second valvulae are rounded (Figs. 9 and 25) with a ridge anterior to the rounded tip. The inner surface of the ridge contains a number of lamellate lobes (Fig. 25). The second valvulae apparently serve as the sawing structure that cuts open the leaf epidermis. They also form a guiding tube with the first valvulae through which eggs pass during oviposition.

2.7. Third valvulae

The third valvulae enclose the first valvulae and second valvulae (Figs. 3 and 4). The third valvulae articulate with the second valvifers via a ramus (r4) (Fig. 27). The outer surfaces of the basal portion of the third valvulae are membranous with pigmentation spots (Figs. 10 and 27). Examined by SEM, the outer surfaces of the third valvulae appear to be smooth (Fig. 28), but the inner surfaces have numerous spine-bearing scales oriented in different directions (Figs. 29, 30 and 33).

3. Sensilla associated with the valvulae and the pygofer

3.1. Trichoid sensilla

Trichoid sensilla are observed on the outer surface of the first valvulae, the pygofer and the second valvifers. Twenty-two trichoid sensilla are found near the basal regions of the first valvulae. These sensilla are of two morphologically distinct types: long, narrow trichoid sensilla (~32 μ m in length)

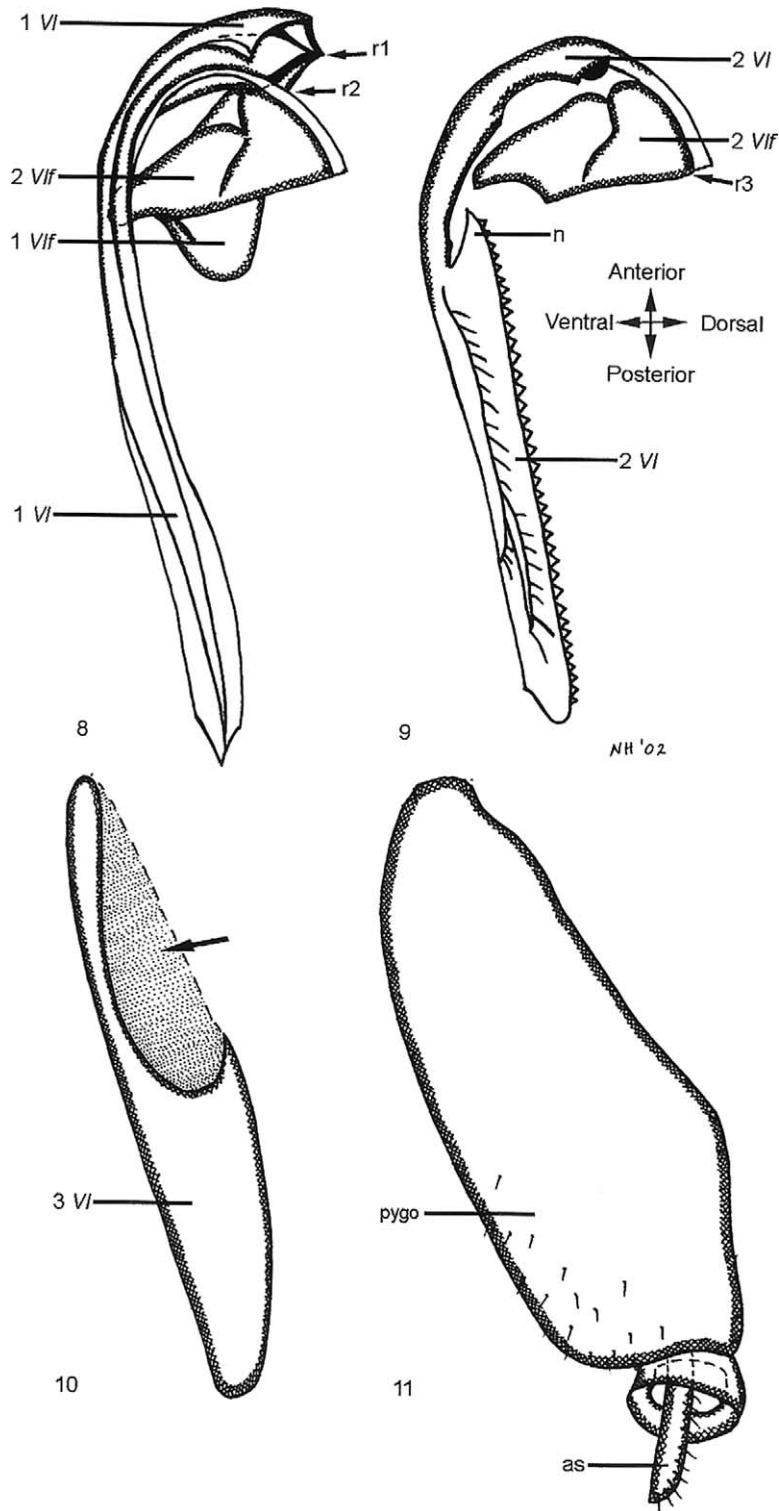


Plate 3. Valvulae of the ovipositor of a female *H. coagulata*. (8) The first valvula (1 VI) with the basal first valvifer (1 Vlf) and the second valvifer (2 Vlf) along with the inner ramus (r1) and the outer ramus (r2). (9) The second valvula (2 VI) with the basal second valvifer (2 Vlf), the ramus (r3), and the distinctive notch (n) at the beginning of the serrated denticles. (10) The third valvula (3 VI) with pigmentation spots (indicated by the black arrow). (11) The pygofer (pygo) and the distal anal stylus (as).

(Fig. 16); and short, wide trichoid sensilla ($\sim 16 \mu\text{m}$ in length) (Fig. 17). The long trichoid sensilla are distributed on the basal regions of the first valvulae and are followed posteriorly by the short trichoid sensilla (Fig. 15). Similarly, a total of fifteen

trichoid sensilla are also found on the outer surface of the second valvifers at the articulation point with the pygofer (Fig. 35). These trichoid sensilla are smooth externally and are approximately $20 \mu\text{m}$ long (Fig. 36). Many trichoid

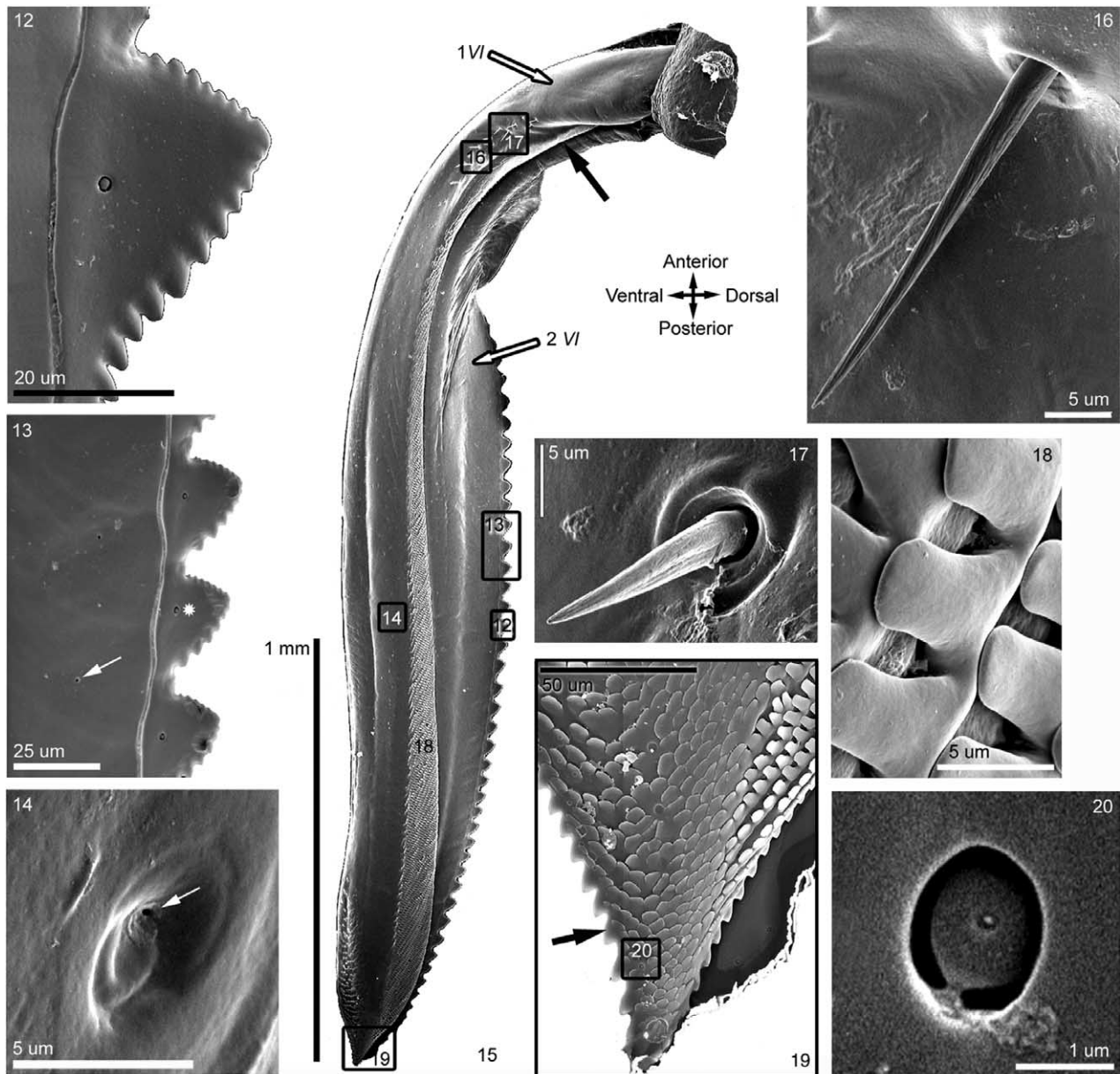


Plate 4. Scanning electron micrographs of the outer surface of the first and second valvulae of a female *H. coagulata*. (12) A single campaniform sensillum located on a serrated denticle of second valvula. (13) Serrated denticles with campaniform sensilla (indicated by the white star) and pores (indicated by the white arrow) located on the outer surface of second valvula. (14) A depression sensillum with molting pore (indicated by the white arrow) on the lateral surface of first valvula. (15) An overview of the external surface and groove (indicated by the black arrow) that connects the first valvula (1 VI) and second valvula (2 VI). (16) A single long trichoid sensillum located on the first valvula (1 VI) near the base. (17) A single short trichoid sensillum located on the first valvula near the base. (18) Square plates that form a comb-like structure on the outer lateral aspect of first valvula. (19) Distal end of first valvula, with serrations (indicated by the black arrow) located at the ventral and dorsal margins, and distal end of the comb structure. (20) A single campaniform sensillum located at the apex of first valvula with molting pore (indicated by the white arrow).

sensilla are also found on the outer surface of the pygofer including smooth trichoid sensilla (Fig. 38); and trichoid sensilla with longitudinal grooves ($\sim 150 \mu\text{m}$ in length) (Fig. 41).

3.2. Campaniform sensilla

Campaniform sensilla, which are dome-shaped sensilla located in a pit, are found on the first valvulae, the second

valvulae, and the second valvifers. A single distinctive campaniform sensillum ($\sim 1.2 \mu\text{m}$ diameter) with a molting pore (Fig. 20 arrow) is found in a pit at the apex of the first valvulae (Figs. 19 and 20). The second valvulae have a campaniform sensillum ($\sim 1.3 \mu\text{m}$ in diameter) on the outer surface of each serrated denticle, beginning with the fifth denticle (Figs. 12 and 13 asterisk). However, five serrated denticles contain two campaniform sensilla. The inner surface of the serrated denticles is smooth and lacks sensilla (Fig. 26).

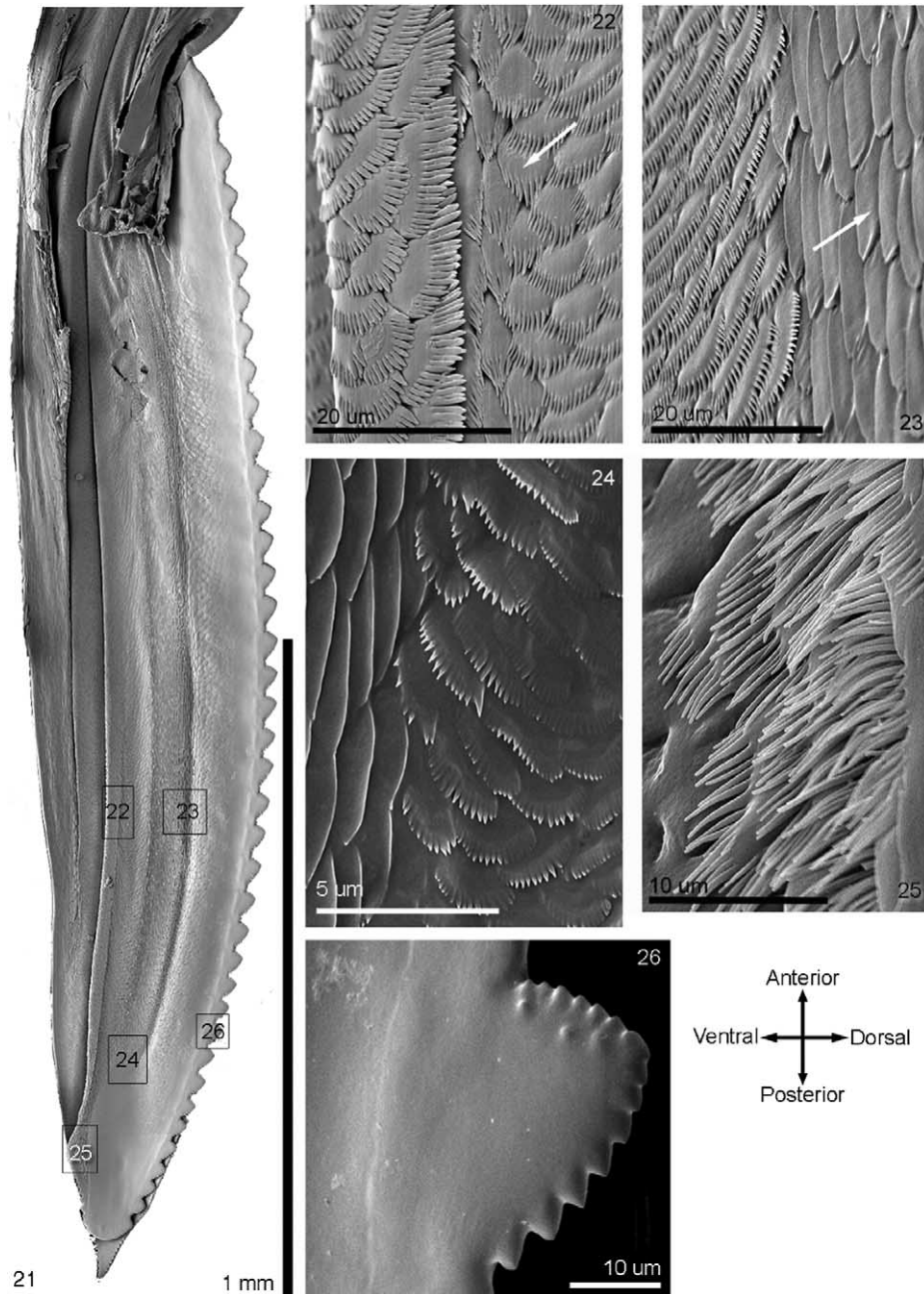


Plate 5. Scanning electron micrographs of the inner surface of the second valvula of a female *H. coagulata*. (21) The inner surface of second valvula of a female *H. coagulata*. (22) Spine-bearing scales (indicated by the white arrow) located on the ventral margin of the inner surface of second valvula. (23) Spine-bearing scales and scales without spines (indicated by the white arrow) on the mesolateral inner surface of second valvula. (24) Reduced spine-bearing scales on the distal mesolateral inner surface of second valvula. (25) Lamellate lobes on the distal ventral margin of the inner surface of second valvula. (26) A single serrated denticle on the dorsal margin of the inner surface of second valvula.

A single small campaniform sensillum ($\sim 1.3 \mu\text{m}$ in diameter) is also observed on the lateral surface of the second valvifers, located dorsally to the trichoid sensilla (Fig. 35 white arrow).

3.3. Coeloconic sensilla

Coeloconic sensilla are found on the inner surfaces of the third valvulae, and the outer and inner surfaces of the pygofer. The third valvulae have many pits or coeloconic sensilla

($\sim 3.4 \mu\text{m}$ in diameter) on the inner surfaces (Figs. 29 and 31). There are multiple teeth-like pegs within each pit of a coeloconic sensillum (Fig. 32). There are a large number of coeloconic sensilla on the outer surface of the pygofer. These sensilla are of two types: a pit ($\sim 4.3 \mu\text{m}$ diameter) that contains approximately 14 pegs (Fig. 42), and a pit ($\sim 1.8 \mu\text{m}$ in diameter) that contains approximately four to six pegs (Fig. 39). On the posterior inner lip of the pygofer there are a large number of coeloconic sensilla ($\sim 2.9 \mu\text{m}$ in diameter) that

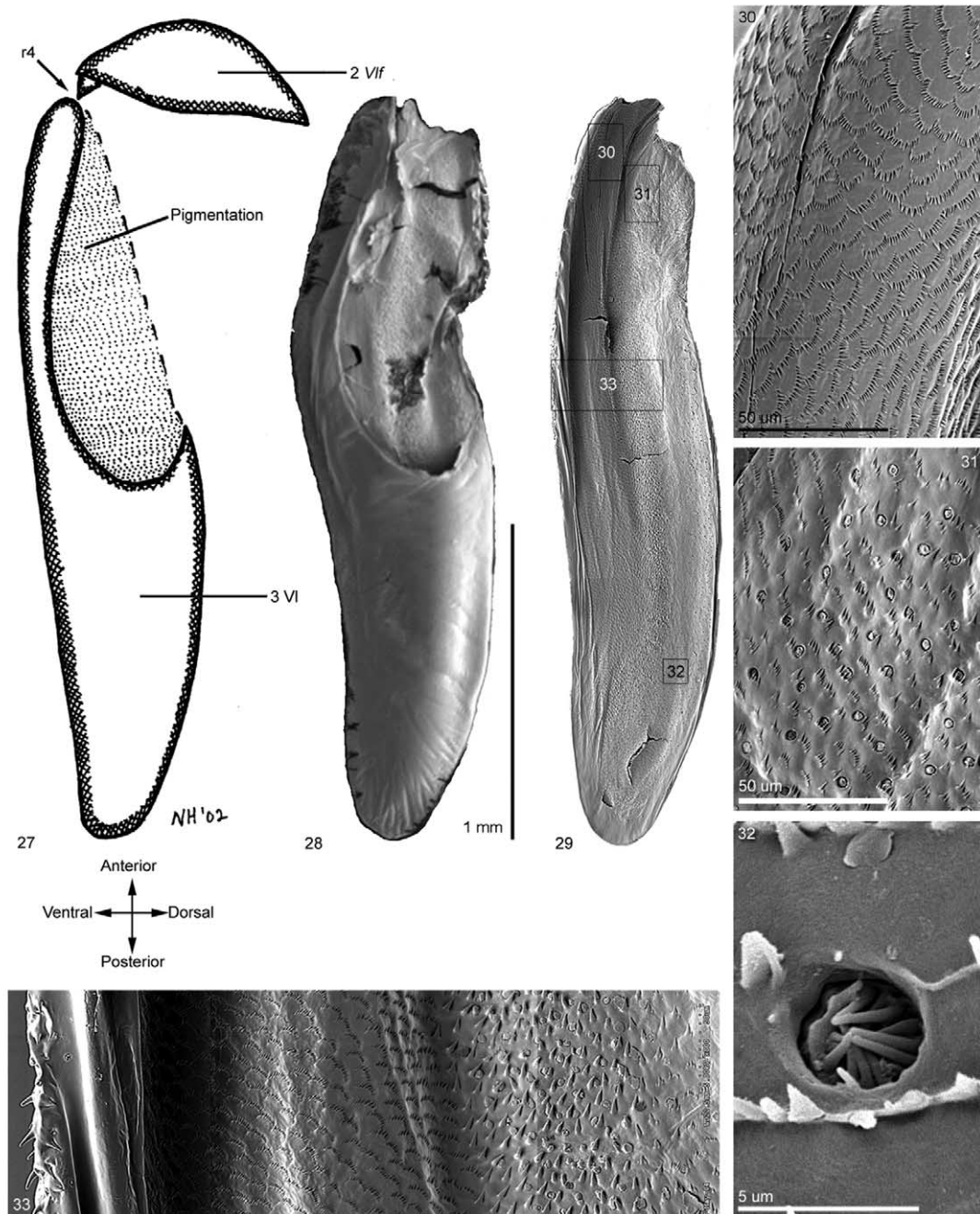


Plate 6. The third valvula of a female *H. coagulata*. (27) Third valvula (3 VI) and second valvifer (2 Vlf) articulating with a single ramus (r4). (28) A scanning electron micrograph of the outer surface of third valvula showing the smooth outer surface. (29) A scanning electron micrograph of the inner surface of third valvula revealing the abundant surface sculpturing and coeloconic sensilla. (30) Spine-bearing scales near the ventral margin on the basal inner surface of third valvula. (31) Many clogged coeloconic sensilla and spine-bearing scales on the inner surface of third valvula. (32) A single coeloconic sensillum on the inner surface of third valvula. (33) An overview of the inner surface of third valvula.

are structurally and morphologically similar to the sensilla located on the outer surface of the pygofer (Fig. 40).

3.4. Cuticular depressions and pores

On the outer surfaces of the first valvulae, posterior to the trichoid sensilla, there are 93 cuticular depressions ($\sim 5.5 \mu\text{m}$ in length) distributed regularly along the length of the first valvulae (Fig. 14). These depressions are oval-shaped and

some appear to contain a single pore ($\sim 0.3 \mu\text{m}$ in diameter) (Fig. 14 white arrow). Near the serrated denticles of the second valvulae, there are minute pits ($\sim 1.0 \mu\text{m}$ in diameter) that appear to be pores (Fig. 13 white arrow).

3.5. Musculature of the ovipositor

Seven muscles are associated with the ovipositor of *H. coagulata* (Figs. 43–46). Muscle one is a dilator originating

on the apodeme of the pygofer and inserting on the common oviduct (Fig. 43). Contraction of muscle one results in the dilation of the genital pore, allowing eggs to move posteriorly into the ovipositor. Muscle two is a retractor originating on the eighth tergite and inserting on the pygofer (Figs. 43 and 46). Contraction of muscle two results in compression of the

pygofer, allowing the ovipositor to drop ventrally away from the body. Muscle three is a depressor originating on the eighth tergite and inserting on the first valvifer (Figs. 43 and 46). Contraction of muscle three results in the pronation of the first valvulae away from the body. Muscle four is a dilator originating on the pygofer and inserting on the third valvulae

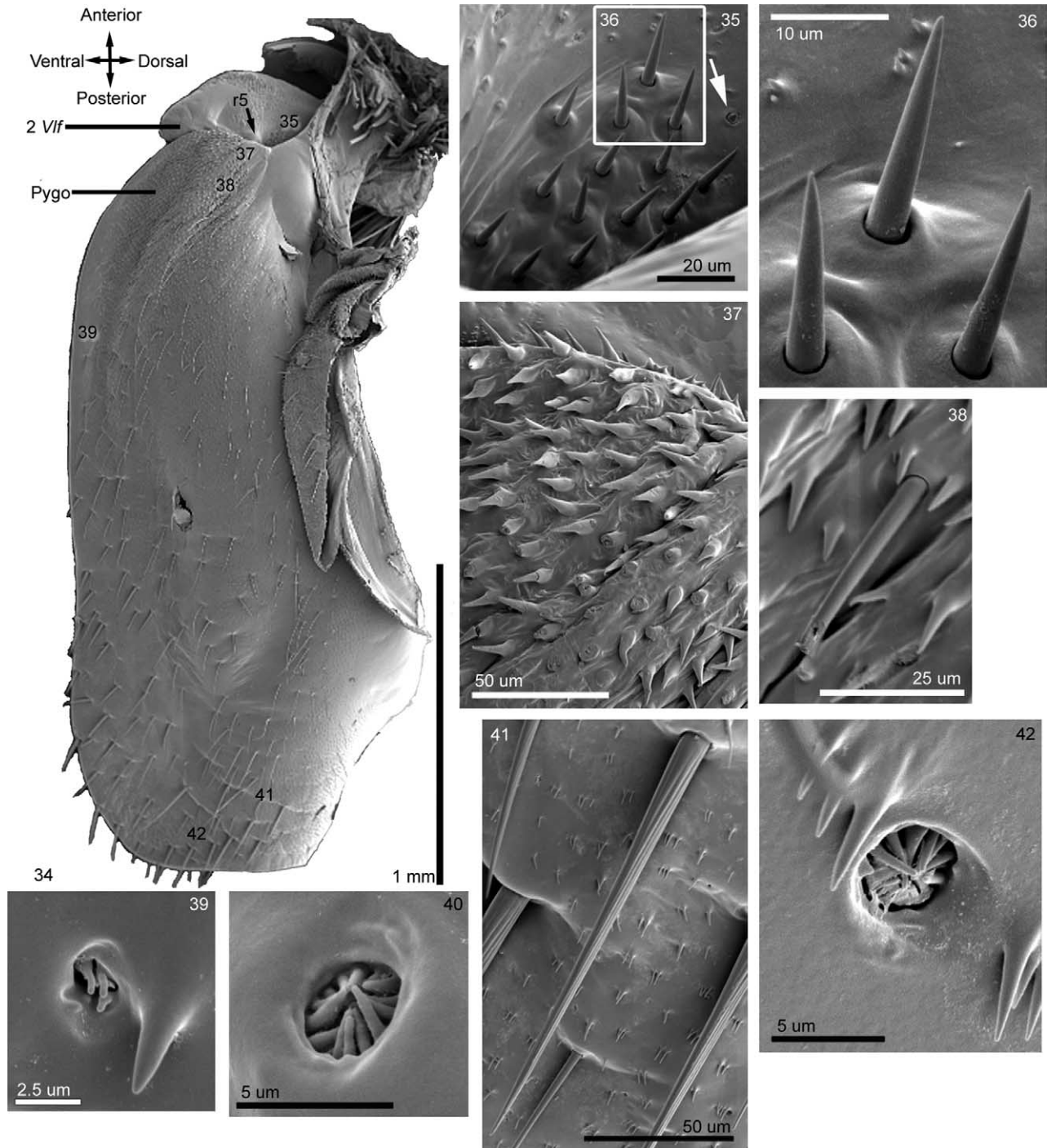


Plate 7. Scanning electron micrographs of the pygofer of a female *H. coagulata*. (34) Scanning electron micrographs of the outer surface of the pygofer (pygo) and second valvifer (2 Vlf), along with the ramus (r5). (35) Trichoid sensilla and a single campaniform sensillum (indicated by the white arrow) on second valvifer (2 Vlf). (36) Trichoid sensilla on second valvifer near the articulation point of the ramus (r5). (37) Spines on the basal margin of the outer surface of the pygofer. (38) A single broken trichoid sensillum on the outer surface of pygofer. (39) A single coeloconic sensillum with approximately four to six pegs, on the outer surface of pygofer. (40) A single coeloconic sensillum with approximately 14 pegs near the distal margin on the inner surface of pygofer. (41) A single trichoid sensillum, near the distal margin of pygofer, with longitudinal grooves. (42) A single coeloconic sensillum with approximately 14 pegs, on the other surface of pygofer.

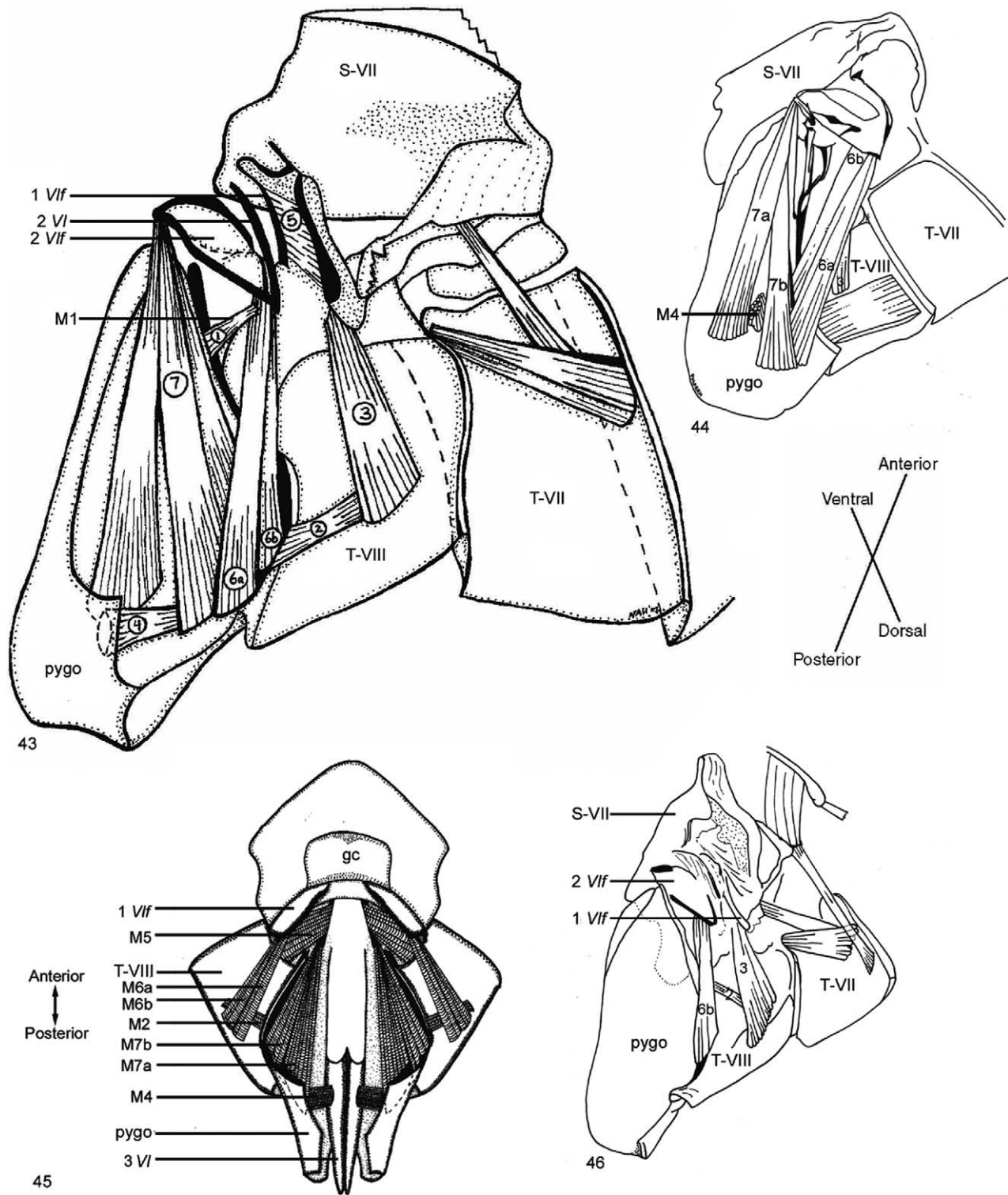


Plate 8. The musculature associated with the ovipositor, pygofer, and valvifers of a female *H. coagulata*. (43) A lateral view of the musculature associated with the valvulae (VI) of *H. coagulata*; 1: muscle one, 2: muscle two, 3: muscle three, 4: muscle four, 5: muscle five, 6a: muscle 6a, 6b: muscle 6b, 7: muscle seven, 1 Vlf: first valvifer, 2 VI: second valvula, 2 Vlf: second valvifer, M1: muscle one, pygo: pygofer, S: sternite, and T: tergite. (44) A lateral view of the ovipositor musculature with first valvifer (1 Vlf) concealed behind second valvifer (2 Vlf); 3: muscle three, 6a: muscle 6a, 6b: muscle 6b, 7a: muscle 7a, 7b: muscle 7b, M4: muscle four, pygo: pygofer, S: sternite, and T: tergite. (45) A dorsal view of ovipositor musculature illustrating the point of articulation of first valvifer (1 Vlf) and third valvulae (3 VI); gc: genital chamber, M2: muscle two, M4: muscle four, M5: muscle five, M6a: muscle 6a, M6b: muscle 6b, M7a: muscle 7a, M7b: muscle 7b, pygo: pygofer, and T: tergite. (46) A lateral view of the musculature associated with first valvifer (1 Vlf) and second valvifer (2 Vlf); after muscle four, muscle 6a, muscle 7a, and muscle 7b were removed; 2: muscle two, 3: muscle three, 6b: muscle 6b, pygo: pygofer, S: sternite, and T: tergite.

(Figs. 43 and 45). Contraction of muscle four results in the dilation of the space between the ventral margins of the third valvulae. Contraction of muscle four also exerts the ovipositor away from the body ventrally. Muscle five is a dilator originating on the posterodorsal portion of the first valvifer and inserting on the dorsal portion of the second valvifers (Fig. 43). Contraction of muscle five causes dilation of the inner space between the paired first valvifers, thus creating a tunnel that an egg can pass through during oviposition. Muscle six is a retractor originating on the apodeme of the pygofer and inserting on the dorsal margin of the second valvifers (Figs. 43–46). Muscle six consists of two muscles, muscle 6a and muscle 6b. Muscle 6a functions as a retractor originating on the posterior aspect of the pygofer apodeme and inserting on the dorsal margin of the second valvifer. Muscle 6b is also a retractor originating on the apodeme ridge of the pygofer and inserting on the dorsal margin of the second valvifer (Fig. 46). Contraction of muscle 6a and muscle 6b results in anteroventral movement of the second valvulae with respect to the long axis of the body and pronates the second valvulae away from the body. Finally, muscle seven is a pronator originating on the posterior dorsal aspect of the pygofer and inserting on the ventral margin of the second valvifers (Figs. 43–45). Muscle seven consists of two muscles, muscle 7a and muscle 7b. Contraction of muscles 7a and 7b draws the second valvulae posteroventrally with respect to the long axis of the body. Movement of the second valvulae also causes movement of the first valvulae anteroventrally.

The hypothesized sequence of muscle action during oviposition is described as follows. (1) Contraction of muscle two retracts the pygofer by pulling the structure anteriorly. (2) Muscle four contracts, causing the separation of the paired third valvulae ventrally along the body mid-line and further exposing the paired first and second valvulae. (3) Muscle three contracts, pulling the first valvifers dorsally, and subsequently causing the first valvulae to depress and exert away from the body. (4) Simultaneous contraction of muscle three and muscle seven results in the ovipositor exerting. The serrated apex of the first valvulae (Fig. 19) pierces the leaf epidermis and the comb on the mesolateral surface (Figs. 15 and 18) serves as an anchor in the leaf epidermis. (5) Muscle 6a and muscle 6b contract, retracting the second valvulae anteriorly toward the body. (6) Relaxation of muscle three and muscle seven, while muscle 6a and muscle 6b contract, causes the ovipositor to move toward the body again, thus initiating sawing into the leaf epidermis. (7) Alternated contraction of muscle three and muscle seven and relaxation of muscle 6a and muscle 6b, causes the second valvulae to slide along the first valvulae assisting in sawing into the leaf epidermis. As muscles 6a and 6b and muscle seven work antagonistically against each other, the serrated denticles of the second valvulae (Fig. 13) move back and forth on the long axis of the body, cutting the leaf epidermis. The simultaneous contraction of muscle three and muscle seven accentuates the sawing of the ovipositor as the second valvulae slide in the groove of the first valvulae (Fig. 15 black arrow). (8) After a slit is made in the leaf epidermis by the first and second valvulae, muscle five contracts causing the

space between the paired first valvifers to dilate. (9) Muscle one contracts, aiding in the expansion of the genital chamber and allowing an egg to pass down the ovipositor. The egg then slides down the middle of the ovipositor in a space between the paired first valvulae and second valvulae. Movement of the egg down the ovipositor during oviposition is probably also assisted by spine-bearing scales that line the inner surface of the second valvulae (Figs. 23 and 24).

3.6. Observations on oviposition behavior

Two video-recordings of oviposition behavior (R. Hix, Pers. Comm.) were observed in order to hypothesize about the relationship between ovipositor action and muscular involvement in oviposition. Based on the morphology of the ovipositor and the musculature of the ovipositor, a hypothetical series of ovipositional events was developed. Before the female *H. coagulata* in both videos began oviposition, they showed a series of stereotypic behaviors. First, the female walks to the underside of the leaf of a host plant and raises both its hindlegs and abdomen away from the plant. Brochosomes droplets are excreted from the anus (Rakitov, 2002; Hix, 2001). As each brochosome droplet is excreted, it is captured by the hindlegs. The hindlegs then move the droplet to a patch of hairs (Hix, 2001) on the forewings. At the conclusion of brochosome application the abdomen drops back toward the leaf, followed by the hindlegs. Droplets of clear excrement, that appear to be urine, are released very rapidly from the anus for about 1 min.

Muscle four, muscle six, and muscle seven contract rhythmically, causing the third valvulae to pulse in and out of the pygofer. Muscle three, muscle six, and muscle seven contract exerting the paired first and second valvulae out of the space between the paired third valvulae. Muscle six and muscle seven antagonistically contract, moving the first and second valvulae against each other. Thus, the tip of the first valvulae is observed moving anteriorly, about one-third the length of the second valvulae. Muscle four and muscle six relax returning the ovipositor to the resting location between the paired third valvulae. Droplets of excrement are excreted for about 1 min.

Next, the insect moves to a new location on the leaf underside and appears to be probing with the mouthparts. The intersegmental muscles and muscle two contract arching the distal end of the abdomen toward the leaf surface. Muscle three contracts exerting the ovipositor toward the leaf surface. Muscle six and muscle seven alternately contract and relax causing the ovipositor to saw into the leaf epidermis. Sawing is enhanced as the abdomen moves back and forth along the long axis of the body. During sawing, denticles on the second valvulae (Fig. 15) are in contact with the leaf surface along with the comb-like region (Fig. 18) and the campaniform sensillum at the apex of the first valvulae (Fig. 20). Muscle three relaxes causing sawing to cease and the ovipositor is removed from the leaf. Muscle two, muscle four, muscle six, and muscle seven contract causing the third valvulae to pulse multiple times.

The insect walks to a new location on the leaf underside. The distal end of the abdomen lowers toward the leaf surface.

Muscle three contracts exerting the ovipositor toward the leaf surface. Muscle six and muscle seven alternately contract and relax causing sawing into the leaf epidermis. The intersegmental muscles contract causing the abdomen to pump. Abdominal pumping most likely indicates several eggs passing down the ovipositor and being placed into the pouch that has been cut into the leaf epidermis, producing an egg mass. The abdomen is parallel to the leaf underside, with the exception of the apex of the abdomen and the pygofer, which are perpendicular to the leaf underside. Muscle three relaxes, retracting the ovipositor from the leaf epidermis. Brochosomes are scraped from the spots on the wings and placed on the egg mass by the hindlegs. At the conclusion of oviposition, brochosomes are applied three more times, the wings are flicked, and the insect walks away from the egg mass.

This pattern, from ovipositor sawing to brochosome application, is observed to be repeated seven times with each mean oviposition time of about 2 min. Dissections of *H. coagulata* female specimens indicate that there are on average 10 ovarioles (ovari) per ovary (ov) ($n=613$; mean \pm SD no. ovari per right ov = 9.7 ± 0.6 ; mean \pm SD no. ovari per left ov = 9.7 ± 0.7). Eggs are deposited in pairs, presumably released from each ovary. Hence, a female has the potential to oviposit 20 eggs per egg mass. In the example described above, the insect would have ovulated seven pairs of eggs in the egg mass. On rare occasions, there was more than one mature egg present in each ovariole, thus the female could oviposit more than 20 eggs in one egg mass.

4. Discussion

The general morphology of the abdominal segmentation, the ovipositor, and the ovipositor musculature of a female *H. coagulata* is similar to that of *Amblydisca gigas* Fowler described by Snodgrass (1933). The external female genitalia have been described for other cicadellid species (Balduf, 1933, 1934; Davis, 1975; Dietrich and Rakitov, 2002; Mejdalani, 1995, 1998; Snodgrass, 1933; Takiya et al., 1999) mostly as a part of taxonomic studies (Dietrich and Rakitov, 2002). Mejdalani (1995) reviewed the literature describing the morphology of the ovipositor of Cicadellidae and related families and concluded that the ovipositor typically consists of three pairs of valvulae; the first two pairs being partially fused and modified for oviposition, and enclosed by the third pair of valvulae. The use of female valvulae as a taxonomic trait was tested by Saxena et al. (1985) who found no significant difference in the morphometrics of the female valvulae of *Nephotettix virescens* Distant, indicating that they were a stable taxonomic trait. One of the distinguishing characteristics of the female valvulae observed herein is the notch at the basal origin of the serrated denticles of the second valvulae of *H. coagulata*. This notch appears to be unique among members of the tribe Proconiini, and may be useful for taxonomic purposes.

This study reports the first SEM observation of the cicadellid ovipositor. Sensilla on the ovipositors of insects provide important information about oviposition behavior and

are much in need of research (Rice and McRae, 1976). SEM examinations of insect ovipositors, and their associated sensilla, have been made in many insect orders, including Diptera (Hooper et al., 1972), Orthoptera (Rice and McRae, 1976), Blattodea (Altner et al., 1977; Yokohari et al., 1975), and Hymenoptera (Hawke et al., 1973; King and Fordy, 1970).

Currently, we do not understand how female *H. coagulata* select suitable host plants for oviposition. The majority of Cicadellidae oviposit in the leaf epidermis, or in plant stems, either singly (*Dalbulus* spp.: Heady et al., 1985; *Empoasca fabae* Harris: Carlson and Hibbs, 1970) or in batches (*H. coagulata*: Hix, 2001). A few Cicadellids oviposit in the soil at the base of the host plant, e.g. *Apogonalia grossa* Signoret (deMenezes, 1978) and *Endria inimica* Say (Coupe and Stoner, 1968a,b). *H. coagulata* oviposit eggs in clusters on the underside of a leaf in the leaf epidermis (Hix, 2001). Surface sculpturing on the valvulae may provide critical assistance during oviposition. The orientation of the spine-bearing scales, on the inner surface of first and second valvulae of the female *H. coagulata* suggests that they may help push the egg down the ovipositor during oviposition. Similar surface sculpturing was found on the valvulae of the membracid *Sextius* spp. and was described as 'ovipositor scales' by Austin and Browning (1981). Spine-bearing scales were also found on the inner surface of the third valvulae in *H. coagulata*. These scales are oriented away from the body cavity, suggesting that they may have a grooming function. 'Pores' similar to those found on the outer surface of the second valvulae of *H. coagulata* were also observed in *Empoasca* spp. by Balduf (1934), who hypothesized that they released lubricant that assisted in the movement of the valvulae against each other during the sawing action of oviposition.

The mechanism for selection of a suitable oviposition host has been studied in some leafhoppers. In *E. fabae*, the act of oviposition was observed to be preceded by probing with the mouthparts (Carlson and Hibbs, 1970). Probing behavior has also been observed in other leafhoppers and it has been hypothesized that sensilla in the mouthparts may be used to determine host suitability for feeding (Backus, 1983). The lamellate lobes on the inner surface of the distal second valvulae are similar in morphology to lamellae described on the mouthparts of *H. coagulata* (Leopold et al., 2003). These lamellate lobes may serve a sensory function. Because of their location at the distal tip of the second valvulae, they could also function mechanically holding the paired second valvulae together during oviposition. A further complexity arises from the observation that a chemical can serve as a stimulus to one species while being a deterrent to another species. Salicylic acid was identified as an important oviposition stimulant for *Nephotettix lugens* Uhler, but it functioned as a deterrent to oviposition in *Laodelphax striatellus* Fallen (Sekido and Sogawa, 1976). These differences between species in response to host stimuli indicate that generalizations should be avoided when examining host selection criteria.

Trichoid sensilla located on the valvulae can potentially serve many functions, ranging from coordinating the activities of oviposition to selecting a suitable oviposition site. Trichoid

sensilla, located toward the base of the first valvulae and posterior to ramus two, may coordinate movement of the first valvulae away from the body as well as to control the degree of rotation of the ovipositor along the long axis of the body during oviposition. The long narrow trichoid sensilla are similar in external morphology to mechanosensory bristles called ‘macrochaetae’ on the body of *Calliphora* (Keil, 1997).

Sensilla and surface sculpturing on the surfaces of the valvulae may function to coordinate oviposition and assist in host selection. During oviposition the comb on the outer surface of the first valvulae of *H. coagulata* macerates the leaf epidermis, and comes into contact with plant volatiles and water molecules in the leaf epidermis. Following the initial probe of the leaf epidermis, the first valvulae are placed between the paired third valvulae. The comb on the first valvulae is then in close proximity to the coeloconic sensilla lining the inner surface of the third valvulae. The proximity along with the pulsing of the third valvulae along the first valvulae could facilitate transfer of plant volatiles and water from the comb of the first valvulae to the coeloconic sensilla of the third valvulae. Thus, this would provide a mechanism for the insect to perceive the chemical properties and host water status of the host plant leaf being probed for oviposition. Furthermore, field observations of *H. coagulata* probing behavior with the ovipositor followed by rejection of the initial host suggests that the coeloconic sensilla on the third valvulae may have a chemosensory function used to distinguish suitable hosts for oviposition. Coeloconic sensilla located on the inner surface of the third valvulae and the inner and outer surface of the pygofer are similar in external morphology to coeloconic sensilla described on the antennae of Acrididae (Ochieng et al., 1998), Sphingidae (Shields and Hildebrand, 2001), and Aphididae (Bromley et al., 1979). Coeloconic sensilla are known to function as thermoreceptors in Culicidae (Davis and Sokolove, 1975), and hygroreceptors and chemoreceptors in Acrididae (Waldow, 1970; Hannon et al., 1996). Thus, the coeloconic sensilla on the third valvulae and the pygofer could function as hygro-, thermo-, and/or chemoreceptors, but TEM examination and electrophysiological study are needed to verify the cell function. It would be of value to further investigate these sensilla using electrophysiological methods.

Structures similar in external morphology to the campaniform sensilla on the first and second valvulae of *H. coagulata* were also described on the ovipositor stylets of a worker *Apis mellifera* L. (King and Fordy, 1970) and the parasitic wasp, *Orgilus lepidus* Muesebeck (Hawke et al., 1973). The ‘dome-shaped sensilla’, with a central pore and surface depressions, on the ovipositor of *O. lepidus* were determined to be mechanoreceptors which were hypothesized to sense pressure and stress from the host (Hawke et al., 1973). The morphological similarity to *O. lepidus* sensilla suggests that the campaniform sensilla on the first and second valvulae of *H. coagulata* might be mechanosensory, but TEM investigation is needed to verify the function of these campaniform sensilla. During oviposition, the first valvulae make initial contact with the leaf surface. The smooth denticles on the ventral margin of the first valvulae initially contact the host leaf and are followed

by the single distal campaniform sensillum. This initial contact is followed by the serrated denticles of the second valvulae, each of which possess a campaniform sensillum. Thus, the campaniform sensilla on the first and second valvulae may sense the mechanical pressure and stress from the plant tissue which would aid in host selection.

Although a general description of the female genitalia and associated musculature in *A. gigas* was reported by Snodgrass (1933), an accurate and detailed study of the female genitalia of *H. coagulata* was needed to understand its reproductive biology. Understanding the functional morphology of the ovipositor and its associated sensilla in *H. coagulata* will facilitate elucidation of host selection mechanisms and could potentially result in the development of novel control methods.

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Appendix A. Glossary of terms

- 1 VI first valvula
- 1 Vlf first valvifer
- 2 VI second valvula
- 2 Vlf second valvifer
- 3 VI third valvula
- abd abdomen
- as anal stylus
- gc genital chamber
- m muscle
- m1 originates on the pygofer apodeme and inserts on the common oviduct, functions as a dilator.
- m2 a retractor, originates on the pygofer and inserts on tergite-VIII.
- m3 a depressor, originates on tergite-VIII and inserts on the first valvifer.
- m4 a dilator, originates on the pygofer and inserts on the third valvula.
- m5 a dilator, originates on the dorsal-posterior portion of the first valvifer and inserts on the dorsal portion of second valvifer.
- m6a a retractor, originates on the dorsal aspect of the second valvifer and inserts on the posterior aspect of the pygofer apodeme.

- m6b a retractor, originates on the dorsal aspect of the second valvifer and inserts on the apodeme ridge.
- m7 a protractor, originates on the posterior dorsal aspect of the pygofer and inserts on the ventral aspect of the second valvifer.
- ov ovary
- ovari ovariole(s)
- ovi ovipositor
- pt paratergite
- pygo pygofer
- r1 ramus that articulates between the first valvula and the first valvifer (inner).
- r2 ramus that articulates between the first valvula and the first valvifer (outer).
- r3 ramus that articulates between the second valvula and the second valvifer.
- r4 ramus that articulates between the third valvula and the second valvifer.
- r5 ramus that articulates between the pygofer and the second valvifer.
- S sternum or sternites
- sbs spine-bearing scales
- T tergum or tergite
- vl valvula
- vlf valvifer

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